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Calling songs and duets of two new species in the *Amblycorypha rotundifolia* complex (Tettigoniidae, Phaneropterinae)

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Abstract

Two new species in the *rotundifolia* complex of *Amblycorypha* from the southern Appalachian Mountains of the USA are described. The calling songs and duets of these two phaneropterine katydids are characterized and discussed. Unlike other members of the *rotundifolia* complex, *Amblycorypha zipticka* **sp. nov.** and *A. monticola* **sp. nov.** have multicomponent calling songs. The songs of *Amblycorypha zipticka* **sp. nov.** have two syllable types that differ in their rates with temperature (1.5/s and 3.8/s at 25°C). Male *A. monticola* **sp. nov.** emit syllables that are grouped into regular echemes. Syllable and echeme rates are temperature dependent. Syllable rates of *A. monticola* **sp. nov.** are the fastest in the *rotundifolia* complex (45/s at 25°C). While calling, males of both species produce ticks that resemble the tick responses of females during duets. As predicted, the timing of the males' ticks within their songs occurs when female replies are expected, and their timing does not change when they call alone or in duets with females. These findings are discussed regarding acoustic countermeasures to competitor eavesdropping and the evolution of signal complexity in the phaneropterines.

Keywords

Complex signals, cryptic species, new species

Introduction

The Phaneropterinae, with more than 2900 species worldwide, is the most speciose taxon within the Tettigoniidae (Cigliano et al. 2025). A major evolutionary driver of phaneropterine diversity is their remarkable signaling system that involves duets. During pair formation, males and females exchange acoustic signals (Spooner 1968, 1995). Although calling males typically locate stationary females by homing in on their tick responses, pair formation can involve both sexes locating each other through phonotaxis (Heller 1990, 1992, Spooner 1995). Duets often exhibit precise timing between the duetting pair's signals (Heller and von Helversen 1986, Stumpner and Meyer 2001, Forrest et al. 2006, Heller et al. 2018).

Additionally, eavesdropping by conspecific males creates the potential for competitive interactions from non-duetting individuals attempting to disrupt the duet. Acoustic countermeasures to eavesdropping, including signal masking, signal mimicry, and deception, are likely to evolve and undoubtedly have increased signal complexity even among closely related species in the phaneropterines (Bailey 2003, Villarreal and Gilbert 2014). These acoustic adaptations to eavesdropping can create a signaling arms race and cause a diversification of songs through sexually selected changes in calling songs within local populations. Small changes in the temporal song structure of duets are enough to cause behavioral isolation and speciation (Heller et al. 2015, Heller et al. 2017, Heller and Hemp 2020).

In the North American phaneropterines, the *Amblycorypha* Stål, 1873 are particularly noteworthy for the diversity of their calling songs, which range from simple, short, single-syllable songs to four-part complex songs of the virtuoso katydids in the *uhleri* complex (Walker 2004). Rehn and Hebard's (1914) treatise on *Amblycorypha* from North America suggested three species complexes in the genus. Species in the *uhleri* complex (5 species) are small. They are easily distinguished from the other two groups by four spots on the margins of their pronota and their calling songs composed of four different acoustic elements (Walker and Dew 1972, Walker 2004). The five species in the *oblongifolia* complex are relatively large with oblong tegmina and simple songs composed of single acoustic elements. In their review of the *rotundifolia* complex, Walker et al. (2003) described two new species (*A. bartrami* Walker, 2003 and *A. alexanderi* Walker, 2003) based on differences in their calling songs and ecology. More recently, Forrest et al. (2023) showed that supposed populations of *A. bartrami* in north Georgia and Alabama, South Carolina, and North Carolina differed in calling song, morphology, and genetics. They added three more species to the *rotundifolia* complex, bringing the current total to seven. Of these seven species in the *rotundifolia* complex, the six from the eastern United States are generally considered cryptic, and calling song is the best characteristic for distinguishing among them.

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In this paper, we describe the calling songs and duets of two new species in the *rotundifolia* complex. Members of the *rotundifolia* complex are flightless, which probably decreases gene flow among populations and thus increases isolation and the probability of speciation. The two new species are found in the southern Appalachian Mountains, where local populations are likely to be separated by elevation gradients and river systems. Indeed, populations of these two locally distributed species are in areas with nearby populations of the more broadly distributed *A. alexanderi* or *A. rotundifolia* Scudder, 1862. The calling songs of the new species are interesting because they include multiple (2–3) acoustic elements, unlike the songs of all other described members of the *rotundifolia* species complex that have only single syllable types. Male songs of both species described here have ticks that resemble the tick responses of their females. The ticks in the songs of male phaneropterines appear to be an acoustic countermeasure to eavesdropping by satellite males (Stumpner and Meyers 2001, Bailey et al. 2006, Heller et al. 2011). One of our goals was to understand the evolution of these complex signals in the *rotundifolia* complex in the context of adaptations to eavesdropping by satellite males. We hypothesized that if male ticks evolved to thwart eavesdropping males from locating and usurping receptive females, these ticks would coincide temporally with female responses. Therefore, we investigated the temporal relationship between male song elements and female responses.

Materials and methods

Fieldwork.—Our fieldwork was mostly conducted at night when the katydids were active. Field sites were in the southern Appalachian Mountains in western North Carolina, USA, and we noted the GPS coordinates of each locale. We collected male katydids by listening for and finding them while they called or by using headlights to search vegetation for males and females in habitats likely to harbor katydids. Some males were recorded in the field before collection. Once collected, katydids were taken into the laboratory and housed in 10 × 10 × 10 cm cages (either clear plastic or screened). The insects were supplied with *ad libitum* water and food (apple, lettuce, oats, or a dry high-protein artificial diet; Gwynne 1988).

Acoustic recordings and analyses.—Calling songs of free-ranging males in the field or caged individuals in the laboratory were recorded with Sennheiser ME66 shotgun microphones and either a Tascam DAP-1 DAT or a Marantz PMD-670 solid-state two-channel recorder. The sampling rate for the digital recordings was either 44 or 48 kHz. Duets were recorded in the lab by simultaneously recording the calling male and responding female on separate channels of two-channel recorders. For duets, microphones were positioned at right angles to one another to minimize signals from the other individual being recorded. To reduce noise and echoes during laboratory recordings, the microphones were positioned 0.5 m from the duetting individuals, whose cages were separated by 1.0 m. In most cases, we covered the substrate between the cages and microphones with Sonex® acoustic foam. We used Audacity® 2.3 or the seewave package in R (Sueur et al. 2008, Sueur 2018, R core team 2020, RStudio team 2020) to characterize the temporal and spectral features of the calling song and to determine the timing relationships between the male's song and the female's tick replies. The ambient temperature (nearest 0.1 °C) for each recording was determined using a precision (traceable) digital thermometer.

In measuring the songs, we looked for repeated patterns in the time waveforms that represent a complete cycle of wing movement (syllable = phonatome, Baker and Chesmore 2020) (Walker et al. 2003). Syllable rates of katydids vary with temperature, and these relationships differ among species and are often used as distinguishing characteristics (Walker 1975). For consistency, one of us (TGF) measured all syllable rates made during the sustained portion of the calling songs (see also Walker et al. 2003). When possible, the rates were based on averages of 10 syllables. However, in some recordings, the sustained series had fewer than 10 syllables at consistent rates. In those cases, the rates were always based on >4 syllables.

Because the calling songs of these two species include ticks resembling female replies during duets, we examined the temporal relationship between the male's ticks, the female's replies, and other elements of the male's calling song. Most temporal parameters of the male calling song change with temperature; therefore, to normalize recordings at different temperatures, we measured the delay of male and female ticks as a proportion of the time between specific song elements. If male ticks evolved as a countermeasure, either to mask female answers to male calling songs or to confuse eavesdropping males, then the timing of male ticks should correspond to the timing of the female replies. We compared the distributions of male ticks while males were calling solo and during duets. To test for differences in means among corresponding tick distributions, we used an ANOVA and Tukey's HSD post hoc test (aov and TukeyHSD functions in R) on logit transformed proportions (Warton and Hui 2011).

Morphological measurements.—We measured morphological characters for both species by positioning preserved, pinned museum specimens and taking digital images (6 Mpix) of their dorsal and lateral aspects. To calibrate our measurements, we placed a scale in the same focal plane as the structures to be measured. We used ImageJ software (Schneider et al. 2012) to measure the following characters (to the nearest 0.1 mm): pronotal length along the midline (PrnL), maximal pronotal width (PrnW), tegminal length (TegL) and width (TegW), hindwing exposure (HwEx), femur and tibia lengths of the hindleg (FemL and TibL, respectively), and for females, ovipositor length (OviL). See also Walker et al. (2003) and Forrest et al. (2023). Measurements for each character were analyzed using ANOVA and Tukey's HSD post hoc test to determine sex-specific differences between the two species (aov and Tukey's HSD functions in R).

Deposition of specimens and recordings.—All specimens are currently housed at the University of North Carolina at Asheville (UNCA). The collection, along with types, will be transferred to the Florida State Collection of Arthropods (FSCA), Gainesville, FL. Recordings will be made available through the Macaulay Library of Natural Sounds at the Cornell Lab of Ornithology and Singing Insects of North America (SINA) website.

Results

Taxonomy.—We begin with the nomenclatural requirements to formally recognize two new species in the *rotundifolia* complex.

Tettigoniidae Krauss, 1902
Phaneropterinae Burmeister, 1838
Amblycoryphini Brunner von Wattenwyl, 1878

***Amblycorypha* Stål, 1873**

Type species.—*Amblycorypha oblongifolia* (De Geer, 1773).

***Amblycorypha zipticka* Forrest & Hamel, sp. nov.**

https://zoobank.org/E344240B-BB48-4E2B-9538-160C5DA3FA1E

Figs 1, 3–6, 12, 13; Table 1

Material examined.—**Holotype:** USA • ♂; North Carolina, Madison Co, Rich Mountain; 35.9271°N, 82.8063°W; 10 Sep. 2006; T.G. Forrest leg.; Au2Rich-M02-2006; DNA (MS-077); REC (2006 Tape01 PGM32); UNCA to be transferred to FSCA. **Allotype:** USA • ♀; North Carolina, Madison Co, Rich Mountain; 35.9271°N, 82.8063°W; 10 Sep. 2006; T.G. Forrest leg.; Au2Rich-F01-2006; DNA (MS-080); UNCA to be transferred to FSCA. **Paratypes:** (27♂, 10♀) USA • 1♂; North Carolina, Madison Co, Rich Mountain; 35.9271°N, 82.8063°W; 3 Aug. 2002; T.K. Goodman leg.; UNCA to be transferred to FSCA • 2♀, 2♂; North Carolina, Madison Co, Rich Mountain; 35.9271°N, 82.8063°W; 14 Aug. 2003; T.G. Forrest and T.K. Goodman leg.; UNCA to be transferred to FSCA • 7♀, 6♂; North Carolina, Madison Co, Rich Mountain; 35.9271°N, 82.8063°W; 28 Jun. 2004; T.G. Forrest and J.A. Hamel leg.; UNCA to be transferred to FSCA • 8♂; North Carolina, Madison Co, Rich Mountain; 35.9269°N, 82.8061°W; 26 Aug. 2004; J.A. Hamel and C.T. Holbrook leg.; UNCA to be transferred to FSCA • 7♂; North Carolina, Madison Co, Rich Mountain; 35.9269°N, 82.8061°W; 1 Oct. 2004; T.G. Forrest, J.A. Hamel and C.T. Holbrook leg.; UNCA to be transferred to FSCA • 2♂; North Carolina, Madison Co, Rich Mountain; 35.9271°N, 82.8063°W; 10 Sep. 2006; T.G. Forrest leg.; UNCA to be transferred to FSCA • 1♀, 1♂; North Carolina, Madison Co, Rich Mountain; 35.9271°N, 82.8063°W; 7 Jul. 2011; T.G. Forrest leg.; UNCA to be transferred to FSCA.

Size measurements (mm).—Holotype: PrnL: 5.2, PrnW: 4.0, TegL: 24.8, TegW: 7.6, HwEx: 3.2, FemL: 23.9, and TibL: 25.8. Allotype: PrnL: 5.7, PrnW: 3.8, TegL: NA, TegW: 7.0, HwEx: NA, FemL: 23.3, TibL: 24.0, OviL: 8.6 (Fig. 1).

Etymology.—This species is named for its multi-component calling song that includes zips and ticks, which are not found in other members of the group.

Common name.—Zip Ticker Round-winged Katydid.

Differential diagnosis.—The best way to distinguish *A. zipticka* from other members of the *rotundifolia* complex is by male calling song. The songs are multi-component and include clicks, zips, and ticks. Clicks have one or two brief impulse trains followed by a longer terminal train of impulses. Clicks temporally resemble song elements of other members of the group, but the relationships of click rate with temperature differ among all members of the complex east of the Mississippi River. Click rates of *A. zipticka* are 1.5/s at 25°C compared to 3.3/s for *A. alexanderi*, 10.0/s for *A. bartrami*, 5.8/s for *A. carolina* Spooner and Forrest 2023, 11.6/s for *A. peedee* Forrest 2023, and 13.0/s by male *A. tallapoosa* Forrest 2023 (Walker et al. 2003, Forrest et al. 2023). *A. zipticka* also produces two other sound elements while calling: zips and ticks. No other members of the *rotundifolia* complex produce zips, each a train of impulses caused by the impacts of the plectrum on a single tooth of the file. Locale might also be used to distinguish this species because it is only known from a single local population in Madison County, NC. However, we expect other undiscovered demes to occur in western North Carolina. Additionally, size could help distinguish *A. zipticka*

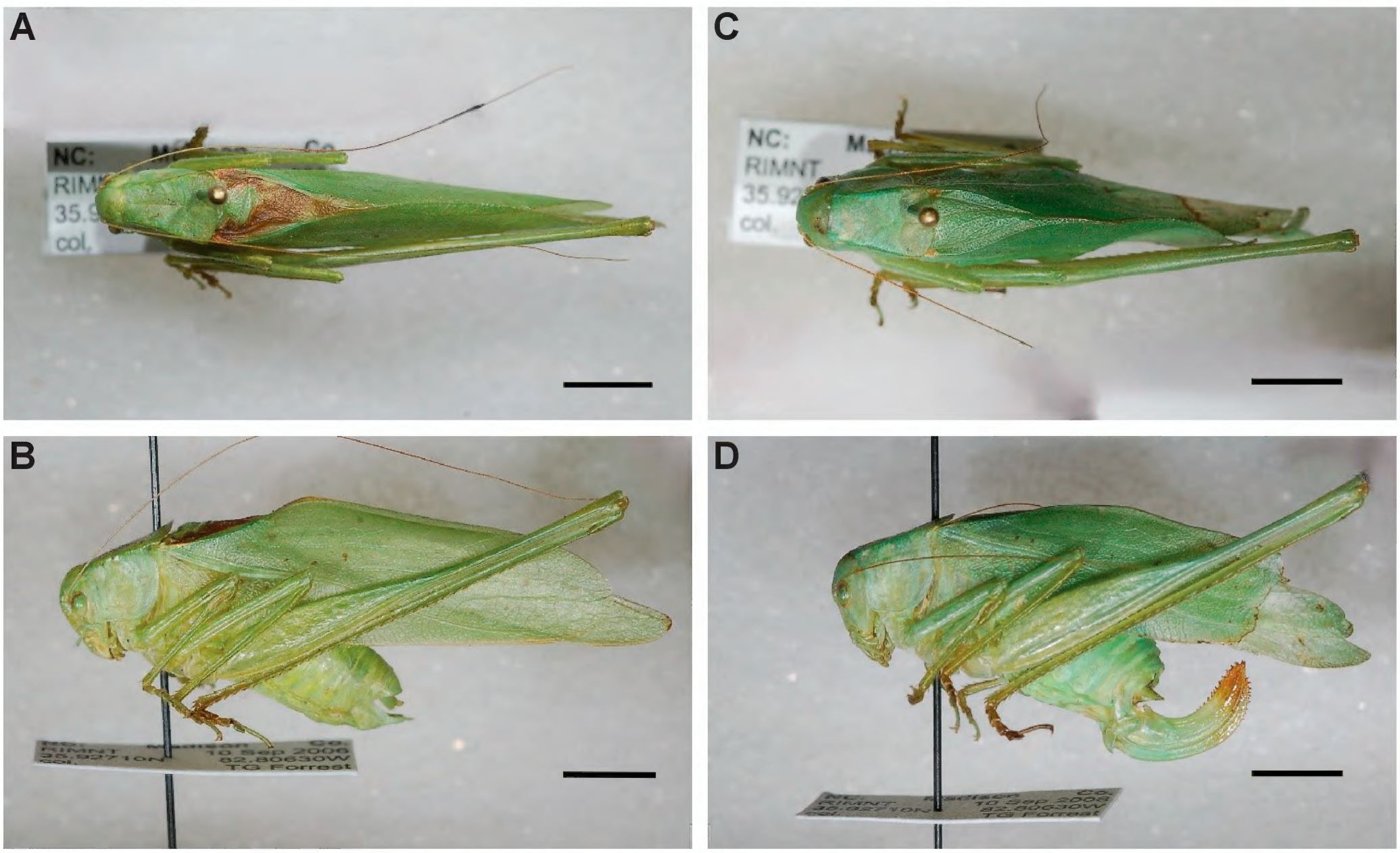

Fig. 1. Holotype (**A.** Dorsal view, **B.** Lateral view) and allotype (**C.** Dorsal view, **D.** Lateral view) of *Amblycorypha zipticka*, the Zip Ticker Round-winged Katydid. Scale bars: 5 mm.

Table 1. Mean (SE, N) of morphological measures (mm) of *Amblycorypha monticola* and *A. zipticka*.*

Sex	PrnL	PrnW	TegL	TegW	FemL	TibL	OviL
Species							
Female							
A. monticola	6.02[a]	4.10[a]	25.10[a]	8.18[a]	24.20[a]	24.90	9.95[a]
	(0.04, 34)	(0.03, 34)	(0.18, 33)	(0.07, 34)	(0.18, 32)	(0.23, 32)	(0.08, 34)
A. zipticka	5.62[b]	3.90[b]	22.40[b]	6.63[b]	23.00[b]	24.20	8.31[b]
	(0.05, 11)	(0.06, 11)	(0.31, 10)	(0.14, 11)	(0.24, 11)	(0.20, 11)	(0.08, 11)
Male							
A. monticola	5.27[a]	3.86	25.20[a]	8.45[a]	23.00	24.20	
	(0.03, 61)	(0.02, 61)	(0.13, 61)	(0.08, 61)	(0.14, 57)	(0.18, 56)	
A. zipticka	4.98[b]	3.79	22.90[b]	7.20[b]	22.70	24.50	
	(0.04, 28)	(0.03, 28)	(0.18, 28)	(0.07, 28)	(0.17, 28)	(0.20, 28)	

* Comparisons of means within each sex were made for each morphological trait. Means within a column followed by different letters are significantly different (ANOVA, Tukey honest significant difference posthoc test, $P<0.05$).

from all other described members of the group because the mean measures of nearly all morphological characters are smaller than those of all other members of the *rotundifolia* complex.

This species is known only from a single locality in Madison County, NC, despite extensive surveys in the area. The population was discovered by Tamara Goodman while surveying for populations of *Scudderia septentrionalis* (Serville, 1838). Interestingly, the calling song of *S. septentrionalis* contains similar acoustic elements (rasps and ticks; see Forrest and Goodman 2008) to the calling song of *A. zipticka*.

Description.—Individuals are typically green and exhibit characteristics of the *rotundifolia* complex (lateral lobe of pronotum with shallow humeral sinus and metasternal lobe wider than long; Walker et al. 2003). Morphological measurements ($\bar{x}$±SE in mm, N) of females average PrnL: 5.6±0.05, 11; PrnW: 3.9±0.06, 11; TegL: 22.4±0.31, 10; TegW: 6.6±0.14, 11; FemL: 23.0±0.24, 11; TibL: 24.2±0.20, 11; OviL: 8.31±0.08, 11. Male size measurements average PrnL: 5.0±0.04, 28; PrnW: 3.8±0.03, 28; TegL: 22.9±0.18, 28; TegW: 7.2±0.07, 28; FemL: 22.7±0.17, 28; TibL: 24.5±0.20, 28 (Table 1).

Male calling songs are composed of three acoustic elements: clicks, zips, and ticks. Clicks have 1–2 short impulse trains followed by a longer terminal train. Zips are each a single train of impulses. Click rate and zip rate change with temperature in linear relationships: click rate = 0.059T-0.010 and zip rate = 0.150T+0.052. Click rates are slower than zip rates (1.5/s vs 3.8/s at 25°C). The typical sequence of song elements during calling is a series of slow clicks that transition to a fast series of zips followed by multiple ticks.

Amblycorypha monticola Forrest & Holbrook, sp. nov.

https://zoobank.org/1A0B8DC4-AB0E-4F3B-AEBD-275C9D2BA656

Figs 2, 7–11, 14, 15; Table 1

Material examined.—**Holotype:** USA • ♂; North Carolina, Buncombe Co., Beetree Gap; 35.7001°N, 82.3989°W; 21 Aug. 2006; T.G. Forrest leg.; Auc-M01-2006; DNA (MS-086); REC (NA); UNCA to be transferred to FSCA. **Allotype:** USA • ♀; North Carolina, Buncombe Co., Beetree Gap; 35.7001°N, 82.3989°W; 21 Aug. 2006; T.G. Forrest leg.; Auc-F01-2006; DNA (NA); REC (NA); UNCA to be transferred to FSCA. **Paratypes:** (61♂, 33♀) USA • 1♂; North Carolina, Buncombe Co., Beetree Gap; 35.7001°N, 82.3989°W; 6 Aug. 2002; T.G. Forrest leg.; UNCA to be transferred to FSCA • 2♂; North Carolina, Buncombe Co., Beetree Gap; 35.7001°N, 82.3989°W; 12 Aug. 2002; T.G. Forrest leg.; UNCA to be transferred to FSCA • 2♂; North Carolina, Graham Co., Nantahala Nat. For.; 35.3878°N, 83.9112°W; 7 Sep. 2002; T.G. Forrest leg.; UNCA to be transferred to FSCA • 2♀,1♂; North Carolina, Buncombe Co., Cane Gap; 35.8099°N, 82.3480°W; 12 Aug. 2003; T.G. Forrest leg.; UNCA to be transferred to FSCA • 2♀; North Carolina, Buncombe Co., Beetree Gap; 35.7001°N, 82.3989°W; 13 Aug. 2003; K.B. Rice leg.; UNCA to be transferred to FSCA • 1♀,3♂; North Carolina, Buncombe Co., Beetree Gap; 35.7001°N, 82.3989°W; 16 Sep. 2003; T.G. Forrest leg.; UNCA to be transferred to FSCA • 7♀,5♂; North Carolina, Buncombe Co., Beetree Gap; 35.7001°N, 82.3989°W; 22 Jul. 2004; T.G. Forrest and J.A. Hamel leg.; UNCA to be transferred to FSCA • 3♀,9♂; North Carolina, Graham Co., Nantahala Nat. For.; 35.3694°N, 83.9168°W; 12 Aug. 2004; T.G. Forrest and J.A. Hamel leg.; UNCA to be transferred to FSCA • 1♀,6♂; North Carolina, Haywood Co., Purchase Knob; 35.5862°N, 83.0737°W; 17 Aug. 2004; T.G. Forrest, J.A. Hamel and C.T. Holbrook leg.; UNCA to be transferred to FSCA • 1♀,2♂; North Carolina, Haywood Co., Balsam Gap; 35.4404°N, 83.0777°W; 22 Aug. 2004; T.G. Forrest, J.A. Hamel and C.T. Holbrook leg.; UNCA to be transferred to FSCA • 1♂; North Carolina, Haywood Co., Spot Knob; 35.3250°N, 82.9638°W; 22 Aug. 2004; T.G. Forrest, J.A. Hamel and C.T. Holbrook leg.; UNCA to be transferred to FSCA • 3♀,6♂; North Carolina, Haywood Co., Cold Springs Creek; 35.7644°N, 82.9766°W; 2 Sep. 2004; T.G. Forrest, J.A. Hamel and C.T. Holbrook leg.; UNCA to be transferred to FSCA • 7♀,5♂; North Carolina, Buncombe Co., Beetree Gap; 35.7001°N, 82.3989°W; 21 Aug. 2006; T.G. Forrest leg.; UNCA to be transferred to FSCA • 1♀,3♂; North Carolina, Haywood Co., Purchase Knob; 35.5862°N, 83.0737°W; 14 Sep. 2006; T.G. Forrest leg.; UNCA to be transferred to FSCA • 2♀; North Carolina, Graham Co., Nantahala Nat. For.; 35.3596°N, 83.9149°W; 23 Sep. 2006; T.G. Forrest leg.; UNCA to be transferred to FSCA • 1♀, 3♂; North Carolina, Madison Co, Max Patch; 35.7968°N, 82.9619°W; 10 Oct. 2006; T.G. Forrest leg.; UNCA to be transferred to FSCA • 6♀; North Carolina, Buncombe Co., Beetree Gap; 35.7001°N, 82.3989°W; 5 Jul. 2007; K.A.M. Dagg leg.; UNCA to be transferred to FSCA • 9♂; North Carolina, Buncombe Co., Beetree Gap; 35.7001°N, 82.3989°W; 5 Jul. 2007; K.A.M. Dagg leg.; UNCA to be transferred to FSCA • 1♀,6♂; North Carolina, Buncombe Co., Beetree Gap; 35.7001°N, 82.3989°W; 26 Aug. 2012; T.G. Forrest and L.D. Block leg.; UNCA to be transferred to FSCA • 2♀,1♂; North Carolina, Madison Co., Bluff Mountain; 35.8514°N, 82.8947°W; 3 Jun. 2017; T.G. Forrest leg.; UNCA to be transferred to FSCA.

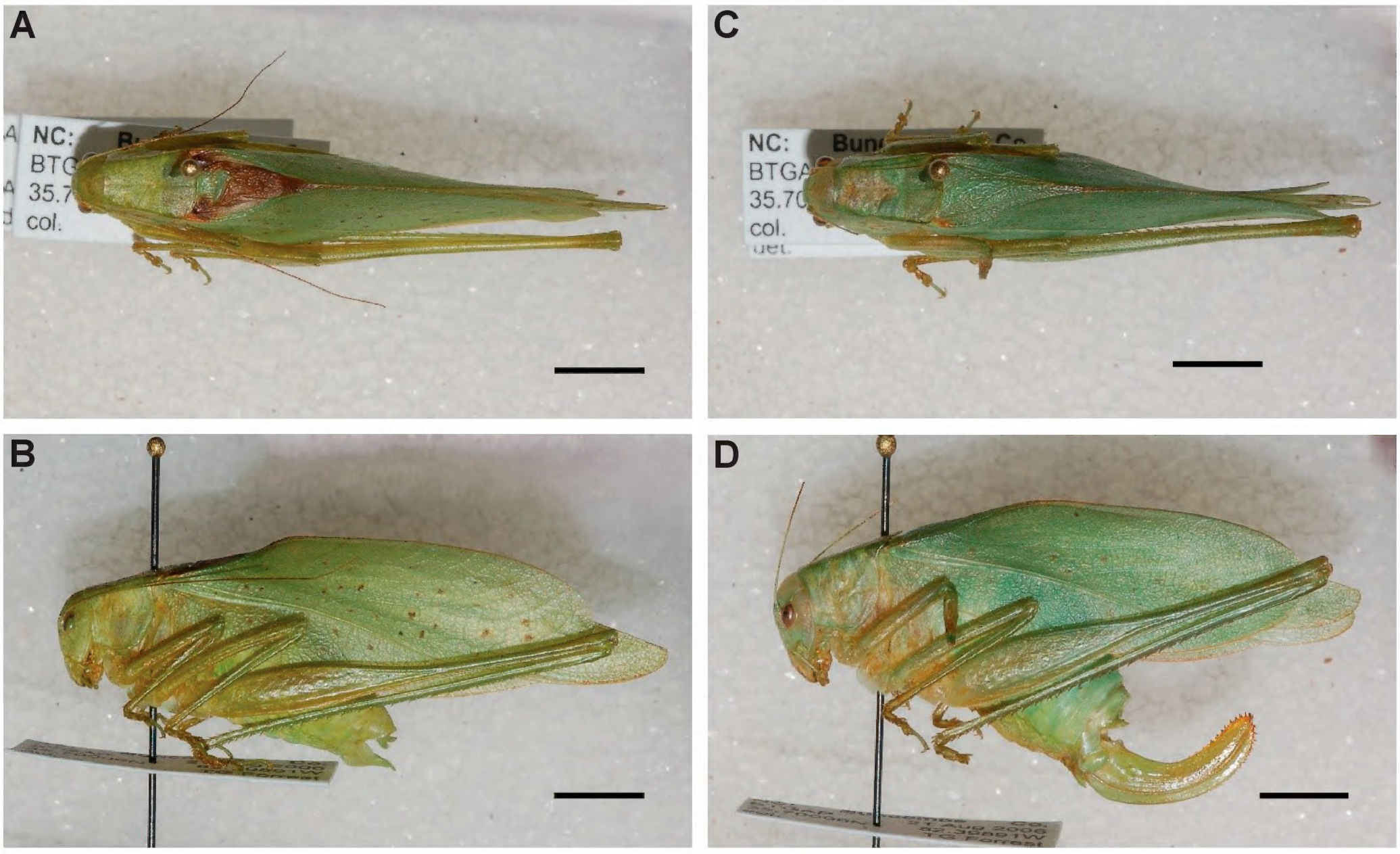

Fig. 2. Holotype (**A.** Dorsal view, **B.** Lateral view) and allotype (**C.** Dorsal view, **D.** Lateral view) of *Amblycorypha monticola*, Montane Round-winged Katydid. Scale bars: 5 mm.

Size measurements (mm).—Holotype: PrnL: 5.3, PrnW: 3.9, TegL: 24.7, TegW: 8.5, HwEx: 4.2, FemL: 23.2, TibL: 24.0mm. Allotype: PrnL: 6.1, PrnW: 4.0, TegL: 23.8, TegW: 8.1, HwEx: 3.1, FemL: 23.1, TibL: 23.7, OviL: 9.8 (Fig. 2).

Etymology.—This species is named for its ecology, which includes mostly high-elevation oak-hickory forests in the southern Blue Ridge Mountains. The specific epithet is derived from Latin monti-: mountain and -cola: dweller.

Common name.—Montane Round-winged Katydid

Differential diagnosis.—Morphologically, *A. monticola* is cryptic with *A. alexanderi* and *A. rotundifolia*, two species whose populations are typically found near those of *A. monticola*. *A. monticola* are most easily distinguished from all members of the *rotundifolia* complex by their unique calling song. Males produce syllables at faster rates, 45/s at 25°C, than any other species in the complex. While calling, 4–7 syllables are grouped into rhythmic echemes, a structure not found in other species' songs. Echemes are constantly produced at slow rates of 1.6/s at 25°C. Males then transition to faster echemes reaching peak rates of 3.1/s at 25°C followed by echemes separated by one or two ticks. Populations of *A. monticola* tend to be at elevations above ~1000 m, whereas other species in the complex are more likely to be found at lower elevations.

Description.—Color is usually green. Lateral lobe of the pronotum with shallow humeral sinus and the metasternal lobes are transverse (see characteristics of the *rotundifolia* complex, Walker et al. 2003). Morphological measurements ($\bar{x}$±SE in mm, N) of females average PrnL: 6.0±0.04, 34; PrnW: 4.1±0.03, 34; TegL: 25.1±0.18, 33; TegW: 8.2±0.07, 34; FemL: 24.2±0.18, 32; TibL: 24.9±0.23, 32; OviL: 10.0±0.08, 34. Male measurements averaged PrnL: 5.3±0.03, 61; PrnW: 3.9±0.02, 61; TegL: 25.2±0.13, 61; TegW: 8.4±0.08, 61; FemL: 23.0±0.14, 57; TibL: 24.2±0.18, 56 (Table 1).

Calling songs of *A. monticola* are emitted as regularly timed echemes consisting of 4–7 syllables. Echemes are constantly produced at ~1.6/s at 25°C, which transitions to a faster series of echemes emitted at 3.1/s at 25°C. In later portions of the fast series, ticks are emitted between the echemes. Within the echemes, the syllable rates are 45/s at 25°C and are the same whether echemes are sung slow or fast.

Comparison of morphology.—Compared to *A. monticola*, *A. zipticka* are smaller in most morphological measures (Table 1). Female *A. zipticka* are significantly smaller than female *A. monticola* in all measures except TibL. Male *A. zipticka* are significantly smaller than *A. monticola* in PrnL, TegL, and TegW, and mean measures are smaller, although not significantly, in every measure except TibL. Comparisons of morphological measures between all members of the eastern *rotundifolia* complex showed that the means of all measures of *A. zipticka* are smaller than the means for all other described species in the complex, except for PrnW in male and female *A. tallapoosa* from north Georgia and Alabama (Walker et al. 2003, Forrest et al. 2023).

Comparison of male songs.—The songs of *A. monticola* and *A. zipticka* are easily distinguished from all other described members of the *rotundifolia* complex in that they have multiple components and the presence of ticks in the male calling song. The male calling song of *A. zipticka* has three acoustic elements: clicks, zips, and

ticks (Figs 3, 4). The typical calling sequence transitions from slow clicks to a fast series of zips followed by a series of male ticks. Ticking may continue into the next series of clicks. Spectra of all three song elements are broadband with most energy between 12 and 15 kHz (Fig. 4B–D, F–H). Clicks and zips are syllables of the song produced during a single wingstroke (see also Shaw et al. 1990, Walker et al. 2003). Clicks consist of 1–2 brief initial impulse trains followed by a longer terminal train (Fig. 5 left) and are produced at an average rate of 1.5/s at 25°C (Fig. 6). Clicks resemble the acoustic structure of the clicks for nearby 'northern' *A. alexanderi*, although the click rates are much slower than those of *A. alexanderi* (1.5/s vs 3.3/s at 25°C, respectively; see Fig. 6). Clicks of 'northern' *A. alexanderi* males are about half the duration of clicks for *A. zipticka* at the same temperature (Walker et al. 2003). During a calling bout of male *A. zipticka*, clicks typically transition to a series of zips that are produced at more than double the click rate 3.8/s at 25°C

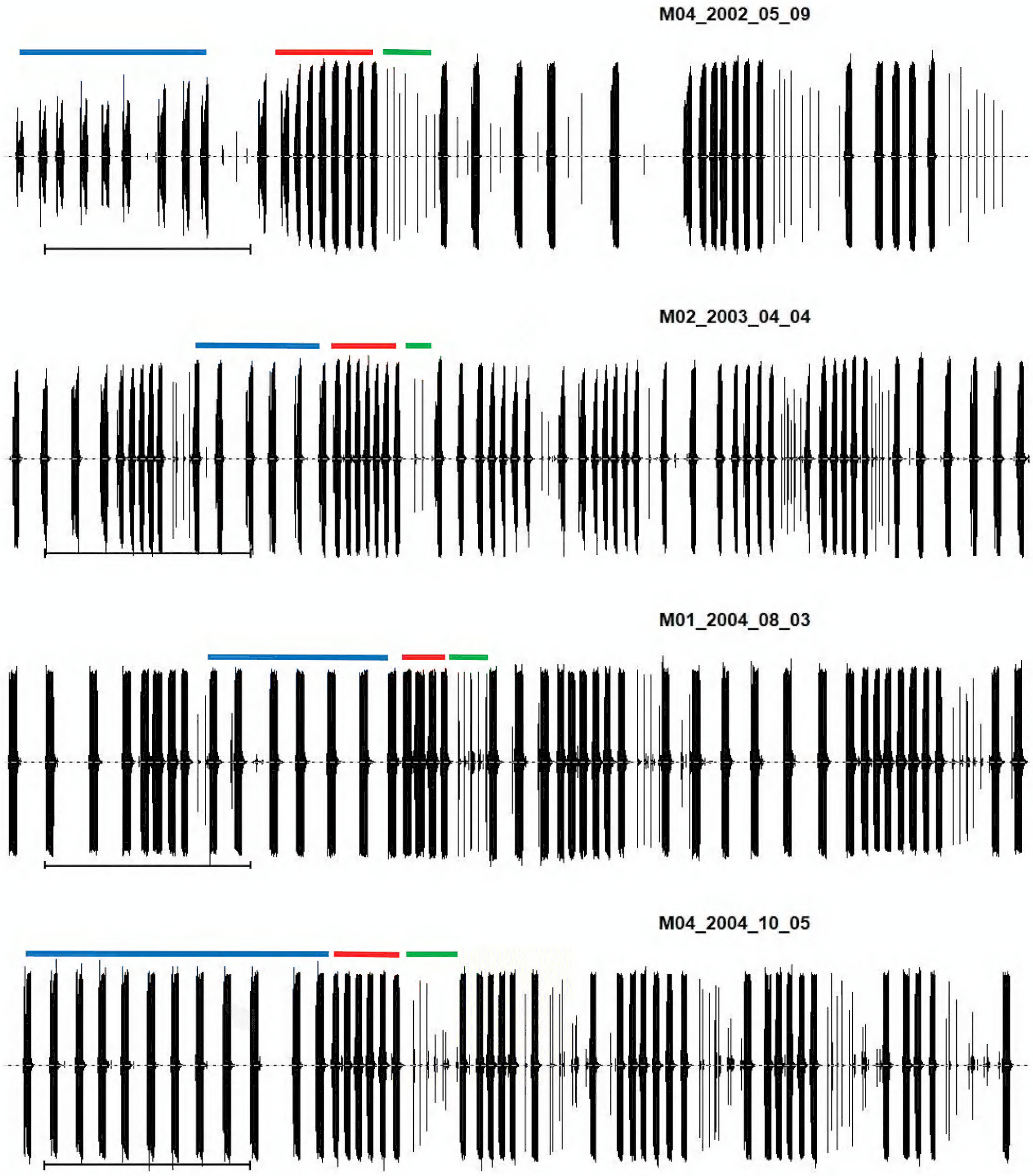

Fig. 3. Oscillograms (25 s) of the calling songs of 4 male *A. zipticka* showing the general temporal structure of calling. Songs consist of two syllable types, clicks and zips. Above portions of each oscillogram, colored bars indicate clicks (blue), zips (red), and ticks (green). Clicks are emitted at slower rates and transition to a faster series of zips that are then followed by a series of brief impulses (ticks). Scale bar: 5 s.

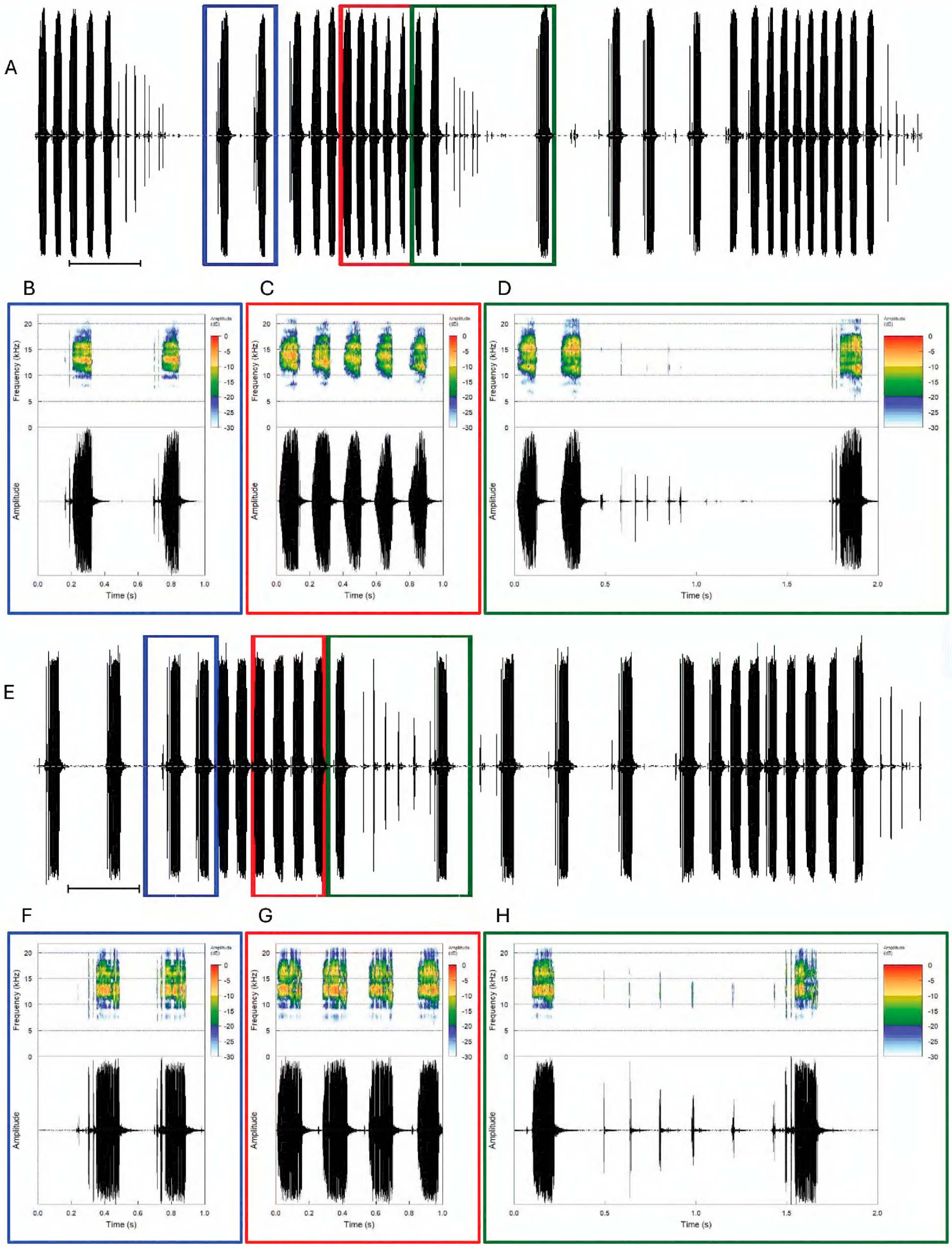

Fig. 4. A, E. Oscillograms (12.5 s) of calling songs of 2 male *A. zipticka*. Scale bar: 1 s. Three different sound elements of the song are highlighted (blue: clicks, red: zips, and green: zip(s) followed by ticks and then a click); **B, F.** Oscillogram and spectrogram of clicks highlighted by blue in **A** and **E**, respectively; **C, G.** Oscillogram and spectrogram of zips outlined by red in **A** and **E**; **D, H.** Sections of **A** and **E** outlined in green showing the transition between last zip to a series of ticks followed by a click.

(Fig. 6). Zips are composed of a single impulse train that resembles the terminal train of clicks (Fig. 5, right). Interestingly, there was greater interindividual variation in zip rate compared to click rate. For example, the zip rates of male #4 were always faster than those of male #3 calling at similar temperatures (Fig. 6; 4.4–5.3/s vs 3.7–4.4/s, respectively). Ticks are one or a few impulses produced by the plectrum moving over one or a few teeth on the file.

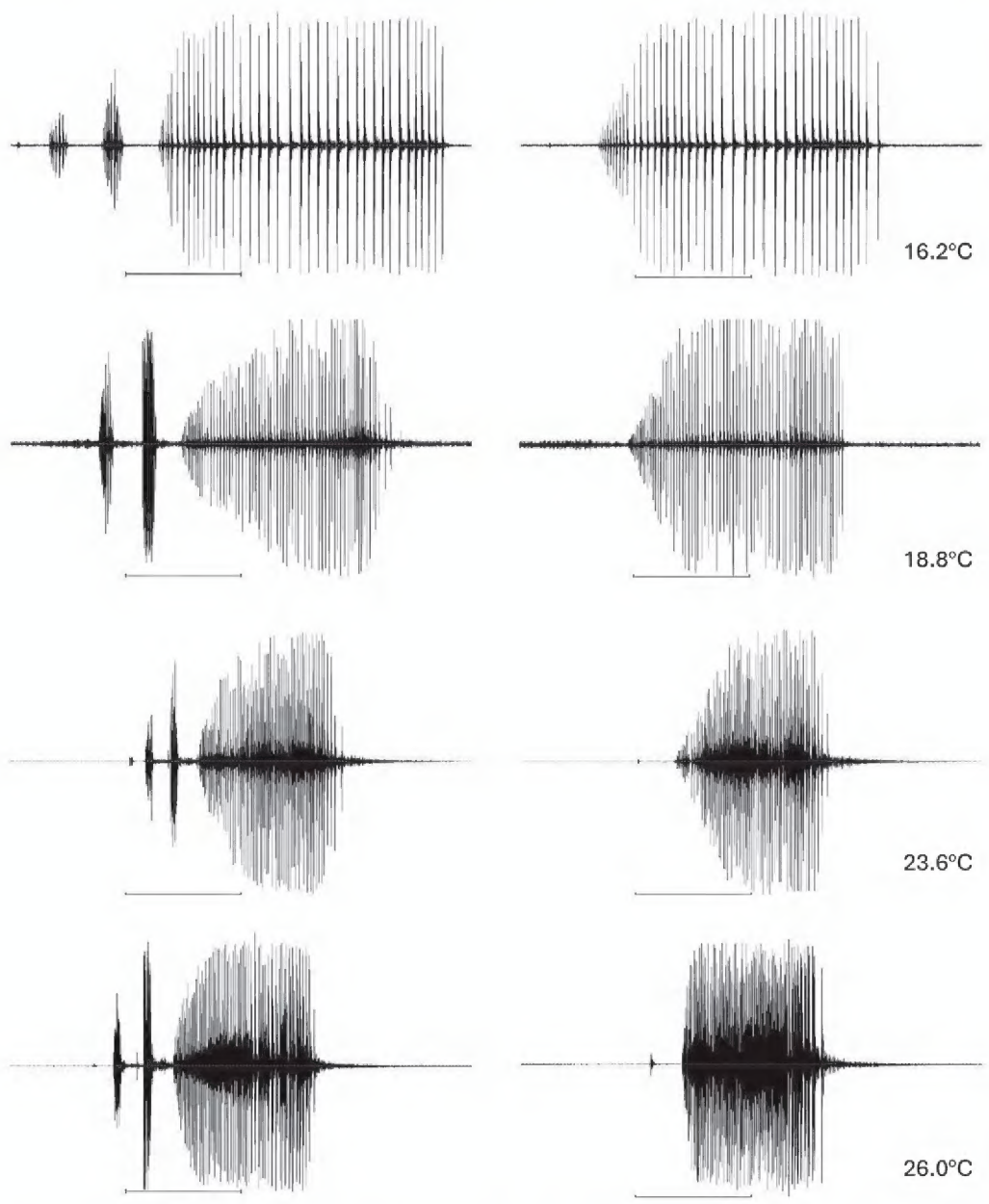

Fig. 5. Fine temporal structure of a click (left) and a zip (right) from the same recording of 4 male *A. zipticka*. Scale bar: 100 ms.

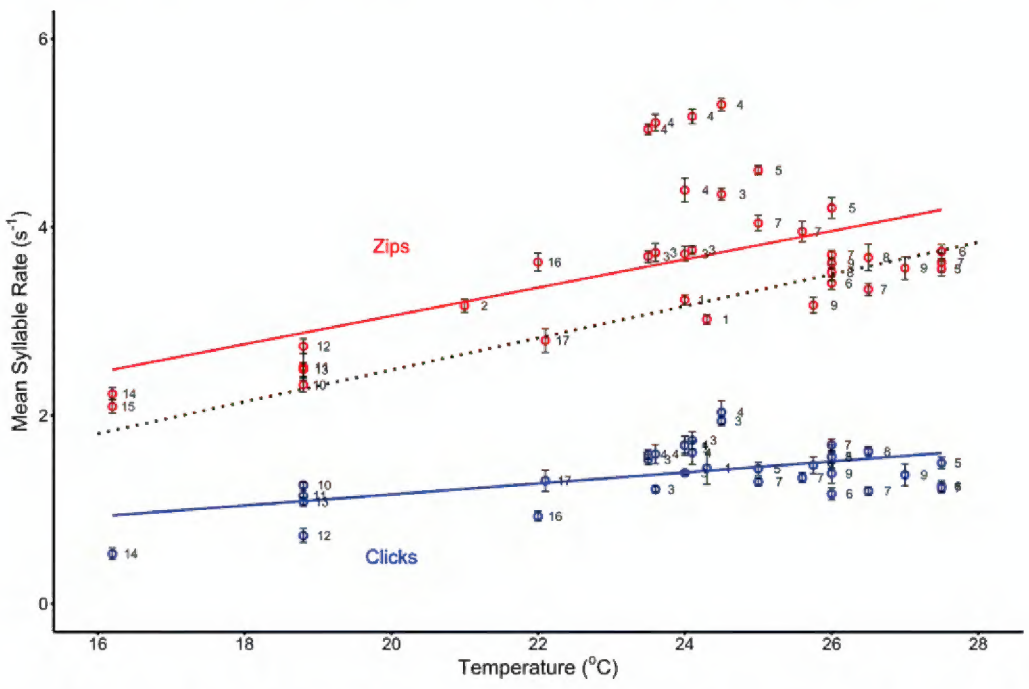

Fig. 6. Mean (±SE) syllable rates as a function of temperature during calling by male *A. zipticka* for clicks (blue fit: rate = 0.059T-0.010) and zips (red fit: rate = 0.150T+0.052). Numbers beside each mean represent the individual (n=17) whose mean rate was measured. Individuals whose click rate and zip rate were calculated at the same temperature are from the same recording. The dotted line is the same function for clicks of *A. alexanderi* from Walker et al. 2003.

Amblycorypha monticola produced both slow and fast sequences of the same sound unit, an echeme composed of multiple song syllables (Fig. 7). Within each echeme, there are 3–8 (usually 4–7) syllables. The closing stroke in each syllable emits an intense train of impulses, most easily observed at lower temperatures when wing cycles are slower. Within the echeme, the first syllable is typically less intense, whereas the terminal 1 or 2 syllables contain more intense and slightly longer duration impulse trains. Male *A. monticola* typically emit echemes at a slow continuous rate while walking among vegetation. Like the song sequence of *A. zipticka*, these slower echemes transition to fast calling sequences of echemes with males emitting 1–4 (usually 1–2) male ticks between later echemes in the sequence (Figs 8, 9). Syllable rates within the echeme are temperature dependent and are produced at an average rate of ~45/s at 25 °C during both fast and slow calling (Fig. 10). The syllable rates of *A. monticola*, about twice that of *A. rotundifolia* (dotted line Fig. 10), are the fastest among the species in the complex. Echeme rates of *A. monticola* are also temperature dependent (Fig. 11), with an average slow rate of 1.6/s and a fast rate of 3.1/s at 25 °C. Echeme rates within the fast sequence accelerated during the first few echemes to a peak rate of 3.1/s at 25 °C, then slowed toward the end of the sequence when ticks are emitted between the echemes.

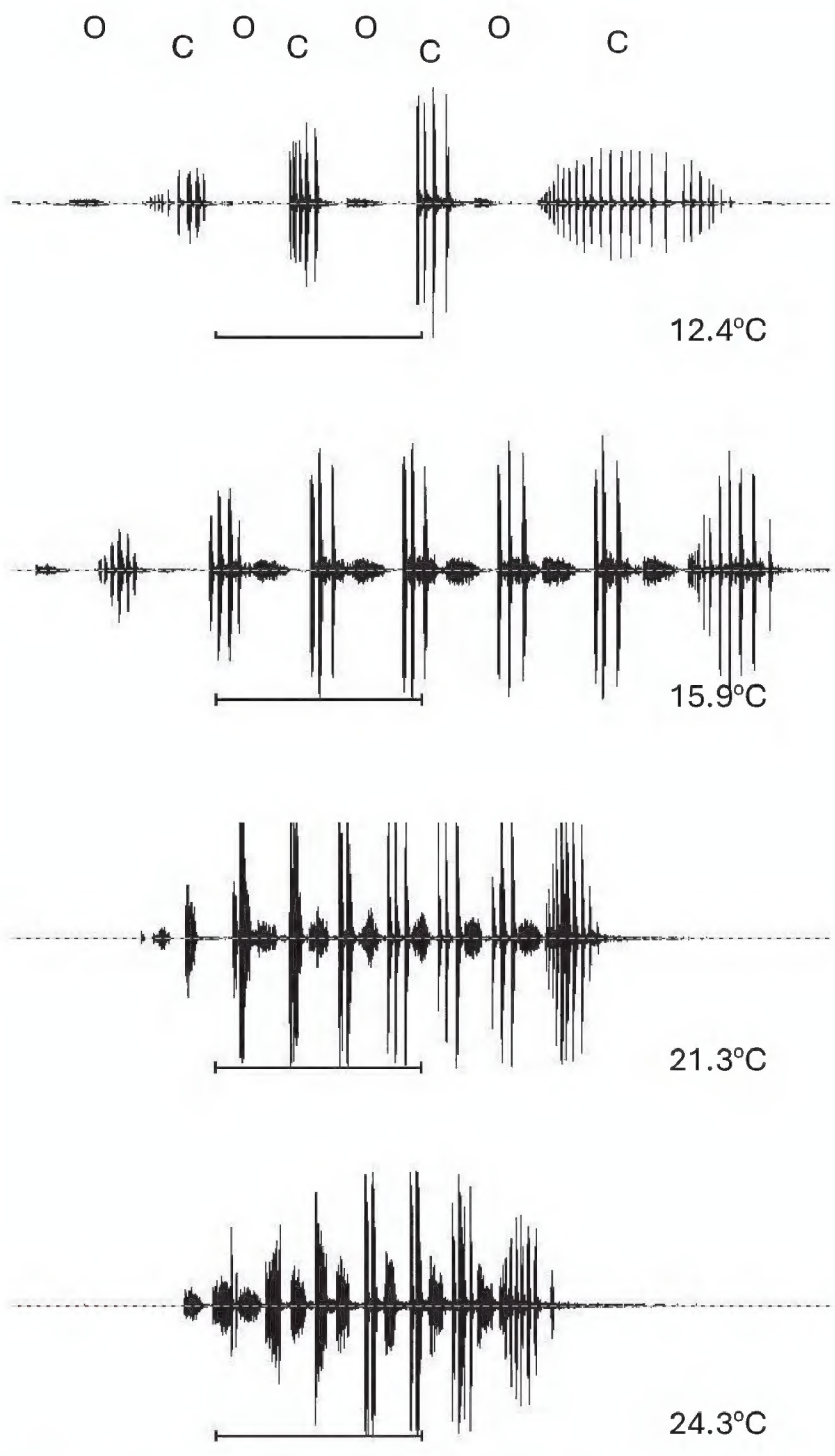

Fig. 7. Oscillograms showing the fine temporal structure of echemes produced by 4 male *A. monticola*. The smaller amplitude sounds between each impulse train are from the opening stroke of the tegmina. Opening (O) and closing (C) strokes are indicated for the top oscillogram. Scale bar: 100 ms.

Male ticks in *A. monticola* and *A. zipticka* are brief impulses that resemble the females' replies during duets. Thus, we will discuss the results from our analysis of male ticks while we describe the results of duets.

Duets.—While calling, male *A. zipticka* emit a series of ticks between the last zip and the following click and then they typically emit another single tick before the next click. During duets, the females in our study responded during parts of the male's song where ticking occurs (see oscillograms of duets in Fig. 12). We have schematically shown the male calling song in Fig. 13A. When males were calling or duetting, the ticks in the first series were uniformly distributed between the zip and following click (Fig. 13B, C). On average, the first tick was emitted at ~25% of the time interval between the zip and following click. Later ticks in the series were emitted at decreasing intervals. The distribution of male ticks appeared uniformly distributed between the two clicks in the sequence with an overall average of ~65% of the time interval between the clicks (Fig. 13B, C). Comparing Fig. 13B and Fig. 13C shows that the distribution of male ticks did not change whether males were solo calling or duetting with females. None of the corresponding mean proportions differed between calling alone or while duetting (Tukey's HSD $p>0.05$). Approximately equal numbers of female tick replies occurred between the zip and the first click and between the subsequent clicks, although the timing of these responses relative to the male signal components differed. Female responses occurred on average at about 50% of the time interval between the zip and click (Fig. 13D) and did not differ from the overall averages of males calling solo or duetting (Tukey's HSD $p>0.05$). Female tick responses were more often given in the last 25% of the interval between the two clicks (Fig. 13D), which differed significantly from ticks produced by males calling solo (proportion = 0.67, Tukey's HSD $p<<0.01$, Fig. 13B) or duetting (proportion = 0.66, Tukey's HSD $p<<0.01$, Fig. 13C).

Ticks emitted by male *A. monticola* generally occurred between echemes during the fast portion of calling. Most often, males produced one or two ticks between echemes (see Fig. 14 for oscillograms of duets). Male calling songs are schematically depicted in Fig. 15A. The distribution of male ticks is shown in Fig. 15B, C. The timing of single ticks was distributed with a single mode, and they were emitted at ~75% of the interval between echemes on average. When two ticks were produced between echemes, their timing was bimodal, with ticks emitted at about 60% and 90% of the time interval. The distributions of male ticks were similar whether males called alone (Fig. 15B) or were duetting with a female (Fig. 15C). Corresponding means of male ticks produced while solo calling or duetting did not differ significantly except for the second ticks when two ticks were emitted (respectively, proportion = 0.86 vs proportion = 0.82, Tukey's HSD $p<0.01$). Although female answers given when males emitted two ticks did not clearly show the bimodality seen in the males' tick distributions, female replies were very similar to male ticks in most respects (Fig. 15B–D).

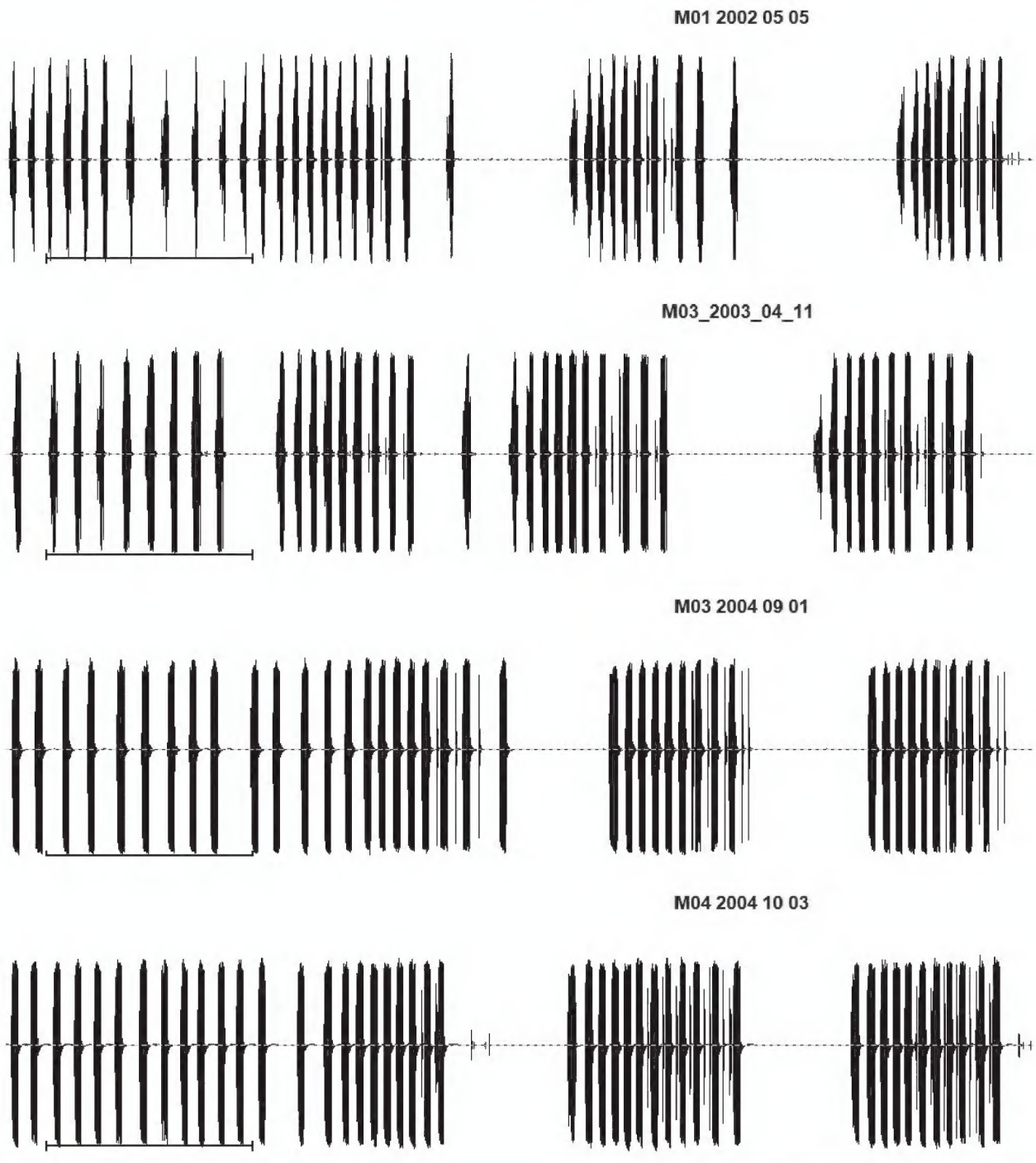

Fig. 8. Oscillograms (25 s) of the calling songs of 4 male *A. monticola* showing the general temporal structure of calling. Songs are continuous slow echemes of 3–8 syllables that transition to short faster series of echemes that include ticks between them in later parts of the series. Multiple short series are often repeated for many seconds. Scale bar: 5 s.

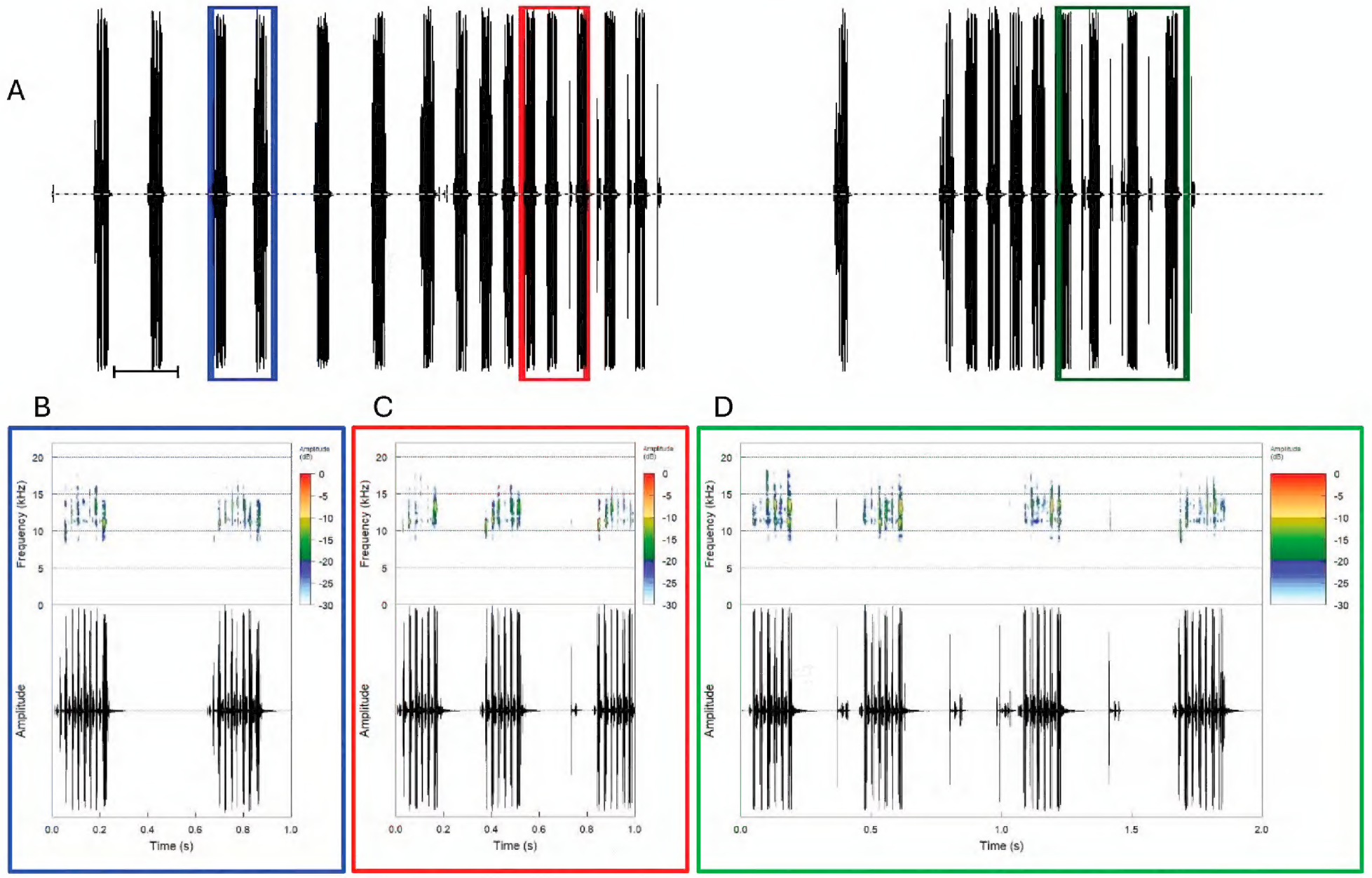

Fig. 9. A, E. Oscillograms (20 s) of calling songs of 2 male *A. monticola*. Scale bar: 1 s. **B, F.** Oscillogram and spectrogram of echemes highlighted by blue in **A** and **E**, with 8 syllables (**B**) and 7 syllables (**F**) typically produced continuously at slow rates during calling. **C, G.** Oscillogram and spectrogram of echemes indicated by the red outline in **A** and **E**, respectively. **D, H.** Echemes highlighted in green with one or two ticks produced between echemes during faster portions of calling.

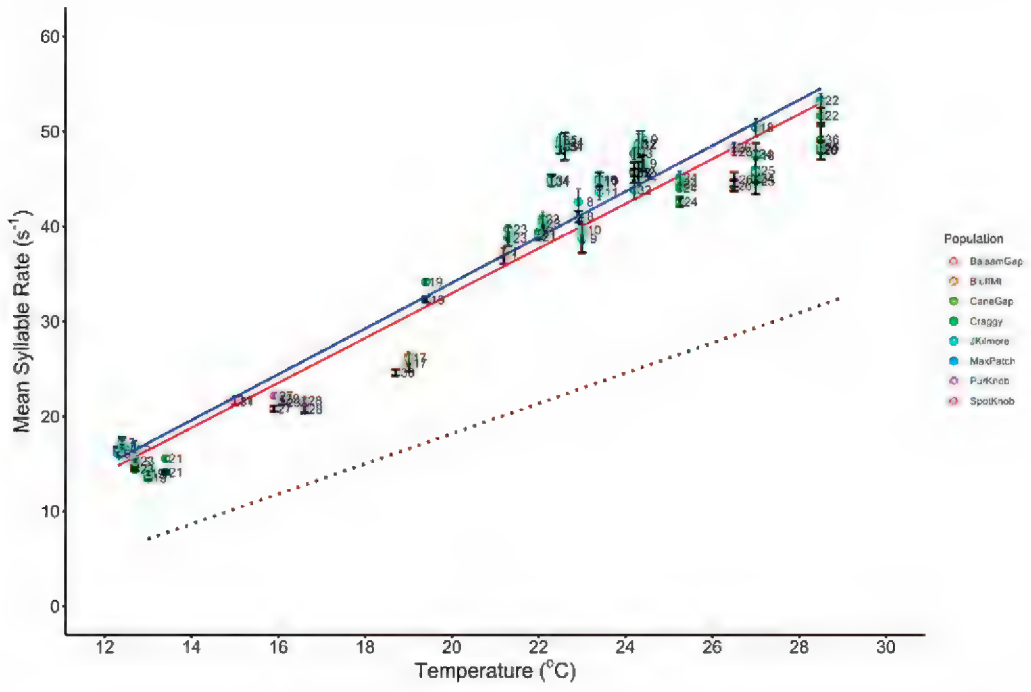

Fig. 10. Mean (±SE) syllable rates within echemes as a function of temperature for individuals from different populations of *A. monticola* in western North Carolina. Numbers beside each mean are the individual (n=29) whose mean rate was measured. Individuals whose rates were calculated at the same temperature are syllable rates from the same recording but measured during slow (blue fit: rate = 2.41T-14.1) and fast (red fit: rate = 2.36T-14.2) portions of the song. Dotted line is the rate function for *A. rotundifolia* (Walker et al. 2003).

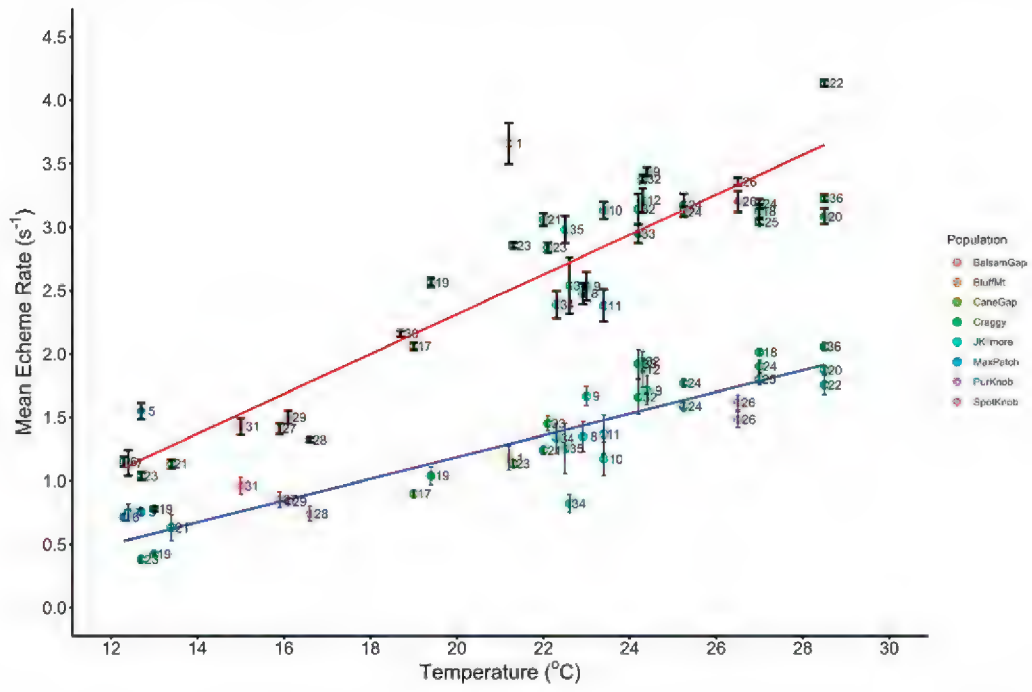

Fig. 11. Mean (±SE) echeme rate as a function of temperature for *A. monticola* males from different North Carolina populations. Numbers beside each mean are the individual (n=29) whose mean rate was measured. Individuals whose rates were calculated at the same temperature are echeme rates from the same recording but measured during slow (blue fit: rate = 0.086T-0.526) and fast (red fit: rate = 0.157T-0.828) portions of the song.

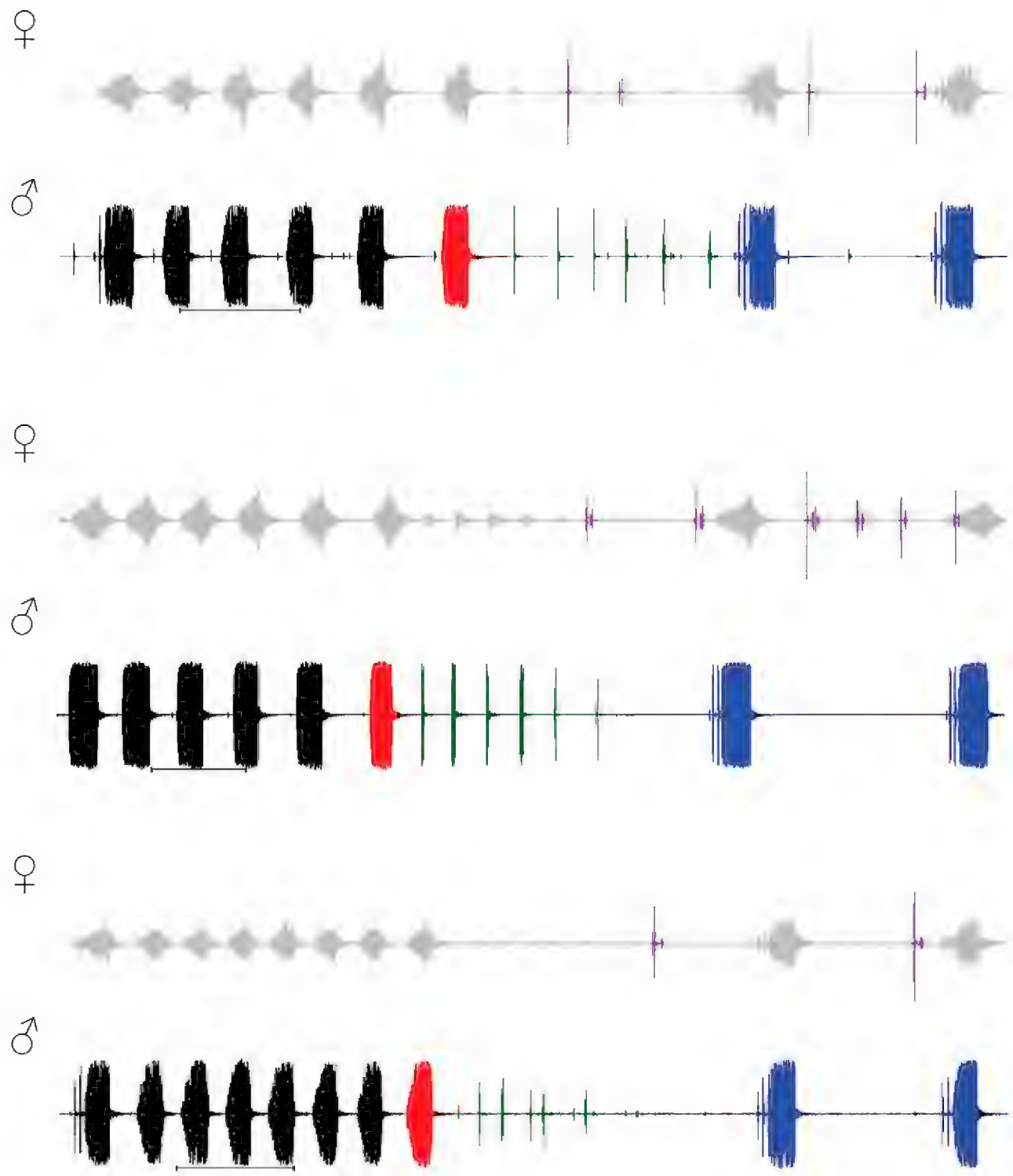

Fig. 12. Oscillograms of portions of duets between 3 *A. zipticka* pairs (female upper trace, male lower trace). The final zip of each male's song is highlighted in red, subsequent clicks are highlighted in blue, and the intervening ticks of the male are highlighted in green. Female tick replies are highlighted in purple. Lower amplitude male songs (grey) are seen in the female traces. Scale bar: 500 ms.

Discussion

Calling song.—The loud, persistent calling songs of male katydids function primarily in pair formation and are under sexual selection through female mate choice and male–male competitive interactions. Females typically respond to specific features of their species' calling songs. Thus, sexual selection through female choice emphasizes and maintains reproductive isolation among species. This important fact means that calling songs are useful clues to identifying species even when morphological differences are lacking and species are otherwise cryptic (Fulton 1932, Walker 1964, Dutta et al. 2017, Heller et al. 2017).

The songs of *A. zipticka* are composed of 'click' syllables that resemble the temporal structure of syllables emitted by most other members of the *rotundifolia* complex, including *A. alexanderi*, *A. bartrami*, *A. carolina*, *A. parvipennis* Stål, 1876, *A. peedee*, and *A. tallapoosa* (Shaw et al. 1990. Walker et al. 2003, Forrest et al. 2023). Clicks have one or two brief impulse trains followed by a longer train of impulses (Figs 4B, F, 5). Click rates increase with temperature, and this relationship differs among species within the complex. In addition to clicks, male *A. zipticka* produce a second syllable type that we term zips, which is unique among species in the *rotundifolia* complex. Zips are a single long impulse train corresponding to a single wing closure (Figs 4C, G, 5). Zip rates also change positively with temperature, but the slope of the increase with temperature is greater for zips than clicks (Fig. 6). Syllable rates at 25°C are 1.5/s and 3.8/s for clicks and zips, respectively. Male *A. zipticka* produce a third acoustic element to their song: brief ticks like those emitted by duetting females (Fig. 4D, H).

The songs of *A. monticola* are unique among members of the *rotundifolia* complex in that their syllables are grouped into rhythmic echemes. Both syllable rate and echeme rate change positively with temperature (Figs 10, 11, respectively). Male *A. monticola* produce echemes at two distinct rates. When moving among vegetation, they produce echemes at a slow rate (1.6/s at 25°C). This transitions to faster rates (3.1/s at 25°C), when echemes are also separated by one or more ticks that resemble the tick responses of females.

Thus, both species have multiple acoustic elements whose rates change with temperature, and these relationships differ distinctly from those of other members of the complex. Based on our analysis of the calling songs of *A. zipticka* and *A. monticola* and a comparison with all other members of the *rotundifolia* complex, we recognized these two new species.

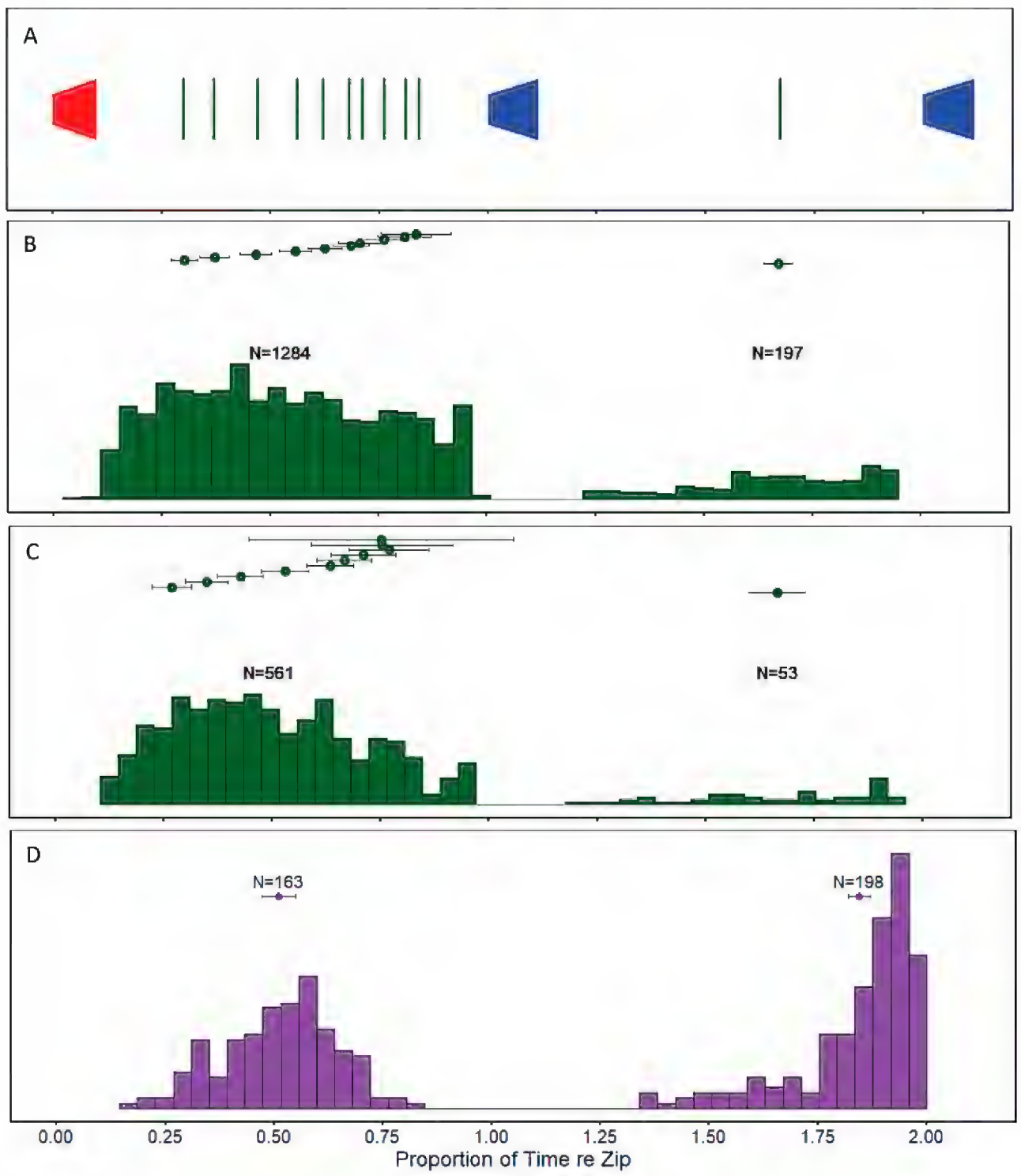

Fig. 13. Distributions of male (green) and female (purple) ticks in *A. zipticka* as a function of the proportion of time between the zip and click (0.0–1.0) and between the first click and next click (1.0–2.0). **A.** Schematic of the final portion of the calling song sequence with 3 song components, zip (red), clicks (blue), and ticks (green). **B.** Overall distribution of male ticks in the song (green) including the mean ± SE (green circles) of individual ticks in the sequences (1–10) between the zip and click. **C.** Same as in **B** but measured during duets with females. **D.** Distribution of female tick responses during the duets in **C**.

Signal complexity in phaneropterines.—Phaneropterine katydids are well known for their complex songs having high diversity in song structure (Heller et al. 2015). Whereas males of most phaneropterines produce only a single syllable type, more complex calling songs with multiple syllable types and phrasing are common. In their global review of the group, Heller et al. (2015) found that more than half of the species surveyed emitted multiple syllable types, and nearly half had multiple types of pauses in their songs. The most complex songs have as many as 5 types of syllables or as many as 7 different types of pauses. A comparison of calling songs across the *Amblycorypha* indicates that the songs of *A. zipticka* and *A. monticola* are intermediate in complexity. Songs of males in the *oblongifolia* and *rotundifolia* groups tend to be monosyllabic, whereas the songs of *A. zipticka* and *A. monticola* have multiple acoustic elements. However, they are not as complex as the songs of members of the *uhleri* complex, which have four elements (Walker and Dew 1972, Walker 2004). Of the four elements in calling songs of males in the *uhleri* complex, type IV syllables are non-descript ticks and are like those given by females during duets. Calling songs of *A. zipticka* and *A. monticola* also have ticks incorporated into their sequences. Based on differences in the structures of other parts of the songs, it seems reasonable that the ticks of *A. zipticka*, *A. monticola*, and those of the *uhleri* group evolved independently.

Duets and female responses.—Phaneropterine communication is noteworthy for duets, where females produce an acoustic signal, usually a brief tick, in response to the male's calling song. Once the duet is formed, the pair exchanges signals back and forth while one or both members of the duet move toward the other. The responses of females are often timed with a specific latency relative to specific portions of the male's song and are thus triggered by some aspect of the calling song. Hammond and Bailey (2003) found that *Caedicia* Stål, 1874 females only responded to the first of two acoustic elements of the male's song and did so with a latency of ~150 ms. In some species, the latency of female replies can be extremely short. Heller et al. (2018) showed that female *Andreiniimon nuptialis* (Karny, 1918) responded with delays of only 20 ms after the beginning of the males' songs, and latencies were <40 ms for female responses in several species of *Leptophyes* Fieber, 1853. *Eurycorypha* Stål, 1873 from northern Tanzania exhibit a wide range of calling songs, and female replies also exhibit complexity (Heller and Hemp 2020). In *E. flexata* Hemp, 2017 and *E. pseudovaria* Hemp, 2017, the songs are simple, and females' response latencies are ~350 ms and 230 ms after the beginning of the song's trigger, respectively.

Female responses within the *Amblycorypha* are quite diverse. Female *A. rotundifolia* respond during long silent intervals between the 'rattling' phrases of their males' songs. The latencies

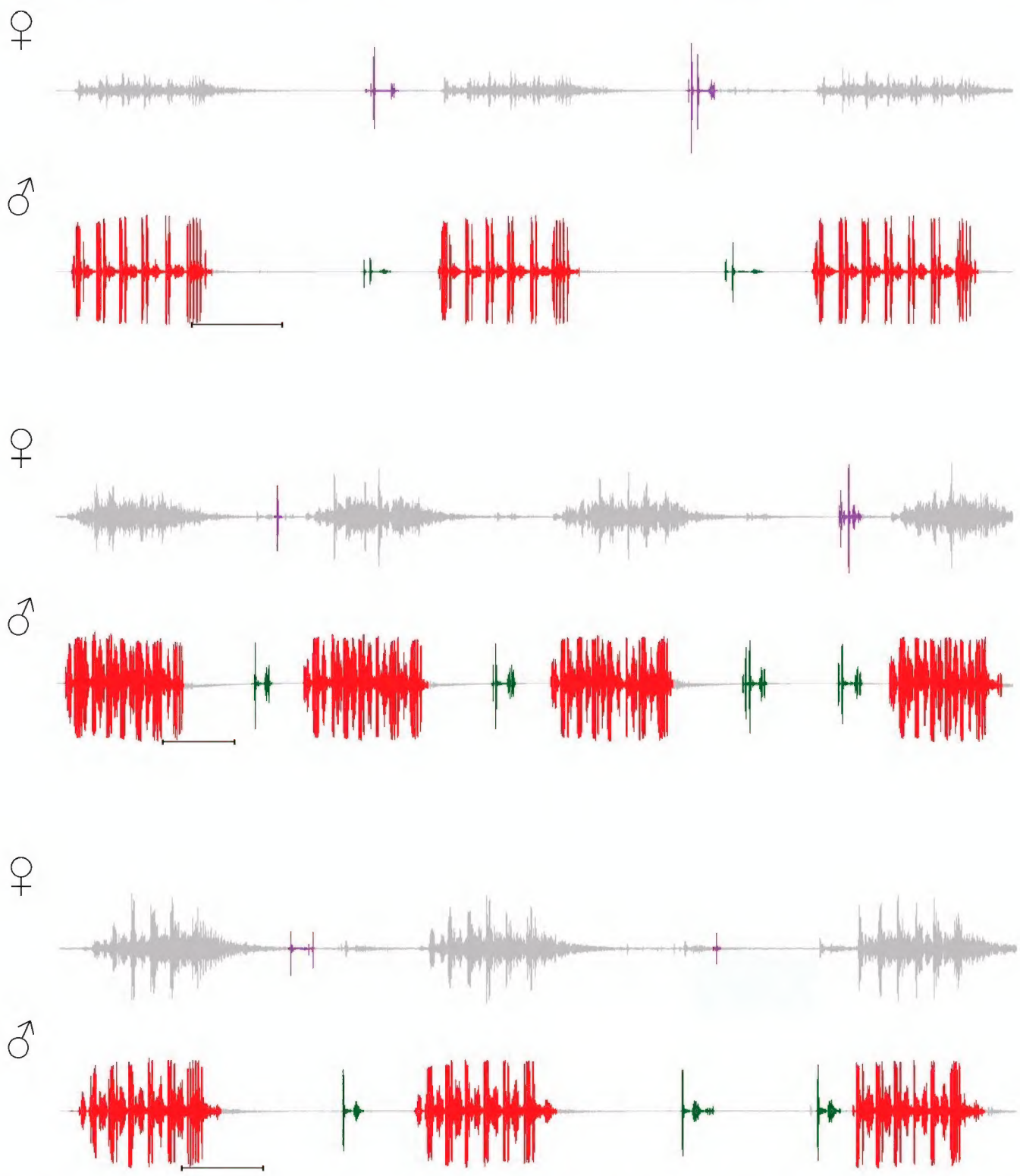

Fig. 14. Oscillograms of portions of duets between 3 *A. monticola* pairs (female upper trace, male lower trace). Echemes of the male are highlighted in red and the males' ticks are highlighted in green. Female tick replies are highlighted in purple. Males' songs are seen at lower amplitudes in the females' traces (grey). Scale bar: 100 ms.

from the beginning of the last syllable in the phrase average about 220 ms but are highly variable, ranging from 12 to >800 ms (Forrest et al. 2006). Latencies of female responses are more precise in *A. alexanderi*: Males produce a series of clicks with an average period of ~300 ms, and females respond between clicks during the last 60% of the series with a latency of ~280 ms (Forrest et al. 2006). In our study, female *A. zipticka* and *A. monticola* responded during the silent intervals between syllables or echemes during that portion of the males' songs where ticks occurred. The distributions of male ticks and female replies did not differ significantly in most cases (Figs 13, 15). In *A. arenicola* and *A. longinicta*, two virtuoso *Amblycorypha* from North America, females nearly always respond during times when males produced their ticks (Type IV syllables, Walker 2004). The timing of female replies with male ticks suggests that male ticks may function as an acoustic countermeasure to eavesdropping by rival males.

Eavesdropping and acoustic countermeasures.—The duets of phaneropterine katydids allow other individuals, particularly satellite males, to detect receptive females through eavesdropping. Under sexual selection, satellite males would be expected to move toward responding females or to produce acoustic signals that disrupt the duet. A sexually selected arms race may ensue, favoring countermeasures that interfere with the ability of satellite males to locate duetting females. In phaneropterines whose songs have multiple acoustic elements, one of the song elements is often a tick (sometimes referred to as clicks or impulses). The function of the ticks in the male songs appears to be an acoustic countermeasure to eavesdropping by males outside the duet (Bailey et al. 2006, Heller et al. 2011). We predicted that if male ticks of *A. zipticka* and *A. monticola* evolved to make it more difficult for eavesdropping males to locate and usurp receptive females, then male ticks should occur at the same time as female responses. If so, then it would also be expected that there would be no change in male songs and their ticks during duetting compared with solo singing. We found that the distribution of male ticks for both species did not differ whether they were solo singing or in a duet and that the temporal distribution of male ticks mimicked that of female tick responses (Figs 12, 13). Male *A. alexanderi*, whose songs are a series of monosyllabic clicks, also do not change the temporal properties of their song when duetting (Forrest et al. 2006). Interestingly, males of another member of the *rotundifolia* complex do change their songs while duetting: In *A. parvipennis*, females preferentially answer and move toward louder males whose songs have longer series of syllables. During duets, males increase the durations of their phrases and decrease silent intervals between them (Galliart and Shaw 1992). We found it intriguing that male *A. zipticka* differed in their fast rate of calling (zips) but not their clicks, which are given at slower rates. Perhaps this characteristic of the song is more dynamic and might be used by females in making mate choice decisions.

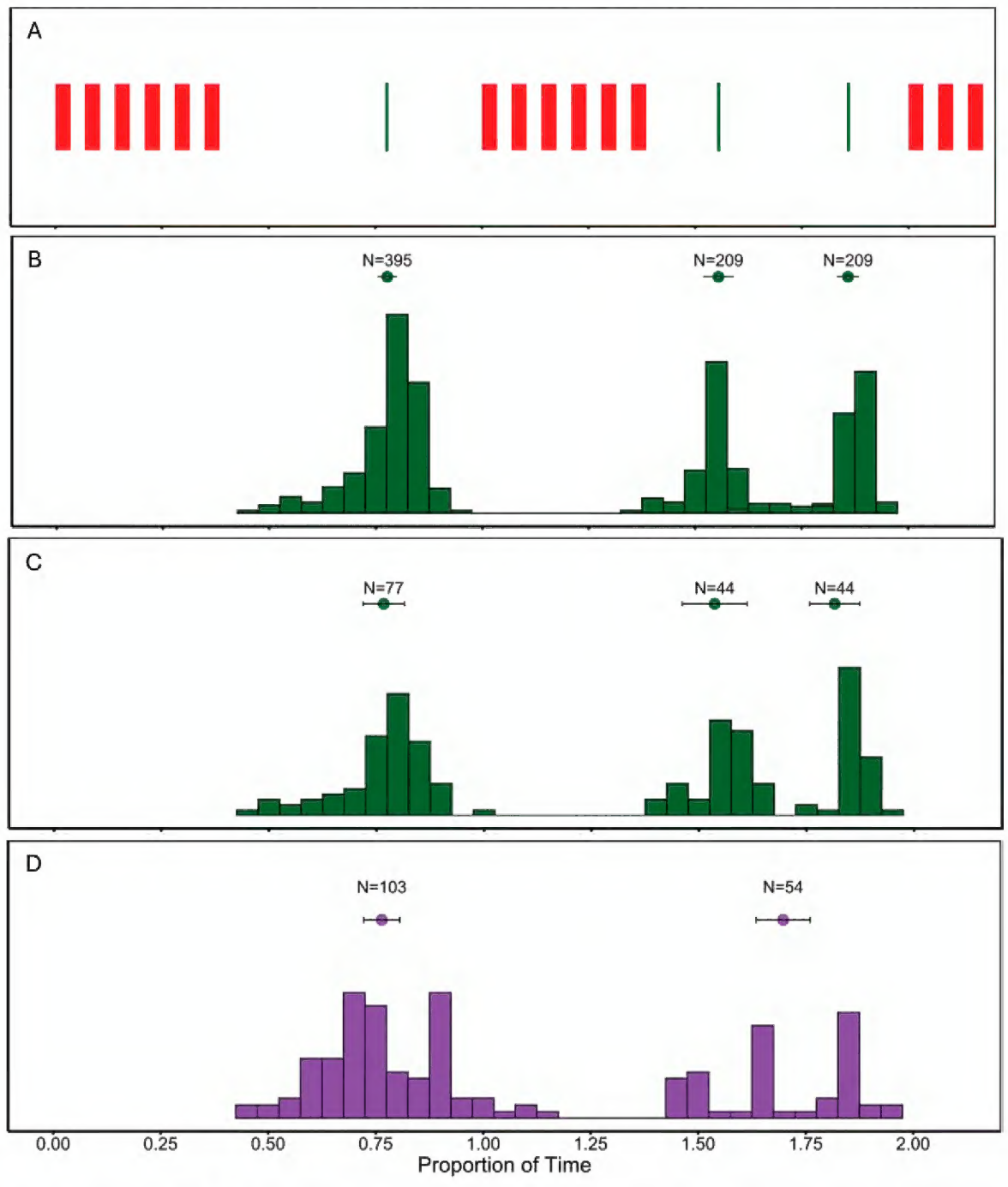

Fig. 15. Distributions of male (green) and female (purple) ticks in *A. monticola* as a function of the proportion of time between an echeme and the next echeme when a single tick or two ticks were emitted, (0.0–1.0) and (1.0–2.0), respectively. **A.** Schematic of the final portion of the calling song sequence with ticks (green) between groups of syllables (red) representing the echemes in the song. **B.** Overall distribution of male ticks in the song (green) including the mean ± SE (green circles) of single ticks (0.0–1.0) and double ticks (1.0–2.0). **C.** Same as in **B** but measured during duets with females. **D.** Distribution of female tick responses during the duets in **C**.

More complex phaneropterine songs have acoustic elements that may function in other contexts such as masking female responses (acoustic mate guarding) or as a trigger for female replies (Stumpner and Meyer 2001, Heller et al. 2015). Hammond and Bailey (2003) studied eavesdropping behavior in *Caedicia*. *Caedicia* songs have two components, and females respond only to the first. The second component is produced during duets and is timed to occur when females reply to the calling male. In their experiment, eavesdropping males did not respond phonotactically to the playbacks of duets containing both song elements or to the single female tick response. It was determined that the masking signal was effective when it occurred <20 ms after the female tick response and if its intensity was >4 dB higher than the female's tick. In later studies of *Caedicia*, alternative mating tactics of eavesdropping males who called during the duet (oversinging) disrupted duet timing, and they sometimes produced calls that included both male and female parts of a duet (Bailey et al. 2006). Although the females of *A. zipticka* and *A. monticola* in our study responded during specific parts of the male calling sequence, their responses were not always consistent, and we did not find any precisely timed female response that would suggest a trigger.

In several phaneropterines with complex songs, males have female-like ticks in their songs or add them to their songs once the duet is formed (Heller and Hemp 2020, Braun 2021). Males of *Xenicola dohrni* (Brunner von Wattenwyl, 1891) produce loud ticks while calling, and females answer with ticks with a latency of about 30–40 ms. Once females respond, the males add a longer rattle-like component that precedes a low-amplitude tick followed 190–350 ms later with a high-amplitude tick (Braun 2021). In the complex duets of *Eurycorypha*, *E. pianofortis* Hemp, 2017 females answer a specific trigger syllable with a delay of ~125 ms but do not answer during the complex echeme that precedes it. This differs from *E. ligata* Hemp, 2017 whose females respond following the echeme with or without a trigger syllable. Females of another species, *E. curviflava* Hemp, 2017, answer two different parts of the males' songs. During duets, males of some *Eurycorypha* species prolong portions of their song so that they overlap female responses. Heller and Hemp (2020) described the 'rivalry' song in *Eurycorypha varia* Brunner von Wattenwyl, 1891. During their observations, an eavesdropping male switched from a calling song to the rivalry song, a series of impulses (ticks?), when the female's replies occurred and would likely interfere with the duetting male's ability to locate the answering female. Although male *A. zipticka* and *A. monticola* songs include female-mimicking 'ticks', these elements are consistent and unchanged during duet. The variability in female response latency and the male song components they answer, along with the fact that males may situationally change their song timing and syntax, adds to the difficulty in characterizing the complex communication system of phaneropterine katydids.

Future work.—One obvious question related to our work on *A. zipticka* and *A. monticola* is how these species, whose songs are intermediate in complexity to other *Amblycorypha*, are related to each other and to other members of the genus. Based on the structure of calling song syllables (clicks) in *A. zipticka*, it seems likely that they have an ancestor with a song similar to *A. alexanderi*. Because *A. monticola* is the only member of the *rotundifolia* complex to produce echemes, it is more difficult to predict an ancestral song. Indeed, the *Amblycorypha* represent an excellent model for understanding the evolution of signal complexity because the signals among the 17 extant species range in complexity from simple monosyllabic songs to the most complex calling songs in North American katydids. A phylogenetic analysis of the genus will allow phylogenetic character mapping of songs and improve our understanding of the evolution of multiple acoustic elements in phaneropterine signals.

Field and laboratory studies are also important to determine the function of multiple syllable types and to examine how or whether male ticks influence phonotaxis by females or males and to what extent ticks deter cuckoldry by eavesdropping males. Additional experiments could test whether females preferentially choose songs of their own males over songs of males from geographically close populations with different signals. Such experiments and observations will elucidate some of the selective forces that increase signal complexity and species diversity in phaneropterine katydids.

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